Trees (2019) 33:777–785
https://doi.org/10.1007/s00468-019-01815-8

ORIGINAL ARTICLE

Seed desiccation tolerance/sensitivity of tree species from Brazilian biodiversity hotspots: considerations for conservation

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Received: 18 June 2018 / Accepted: 16 January 2019 / Published online: 23 January 2019

Abstract

Key message **Seed banking is an essential tool for species conservation. However, two world's biodiversity hotspots in a megadiverse tropical country have high percentage of short-lived seeds, requiring new strategies for preservation.**

Abstract Information on seed storage behaviour is crucial for conservation, especially on highly impacted biomes. Thus, this study aimed to investigate seed desiccation tolerance/sensitivity in native tree species of two world's biodiversity hotspots, Atlantic Forest and Cerrado. We assessed seed storage behaviour for 11 species. The tests were conducted immediately after seed collection at 12% and 8–5% of water content followed by 3 months of storage at − 18 °C. In addition, we retrieved data on the literature about water content after dispersal and storage behaviour of seeds for several tree species native from these hotspots. It comprised 79 species from 30 families. From this total, 47.4% of species produced orthodox seeds, 19.2% intermediate, and 33.3% recalcitrant seeds. All species from Lauraceae produced recalcitrant seeds. Most of studied species produce long-lived orthodox seeds; however, a high percentage of species produce sensitive seeds. Species producing short-lived seeds require non-conventional storage methods. Information on seed storage behaviour is fundamental for species management, especially in tropical areas, where the number of recalcitrant species is high. Thus, seed banking and other conservation strategies must be improved to avoid species loss. Technologies to improve storage of recalcitrant seeds are discussed.

Keywords Biodiversity hotspots · Desiccation tolerance · Conservation · Orthodox seeds · Recalcitrant seeds · Restoration

Introduction

Amongst the 25 biodiversity hotspots around the world two of them are in Brazil, the Atlantic Forest and Cerrado (Myers et al. 2000). The Atlantic Forest consists of three vegetation types: Ombrophylus Dense forest; Semideciduous and Deciduous Stationary forest; and Ombrophylus Mist forest (Colombo and Joly 2010). Atlantic Forest is considered one of the richest biomes worldwide and has a high endemism level (Myers et al. 2000). The Cerrado (Brazilian savanna) landscape varies from grassland to dense woodland (Ratter et al. 1997), and regarding species number and endemism, it is considered the richest savanna in the world (Klink and Machado 2005). Because of these features, the two biomes are classified as global priority areas for conservation (Myers et al. 2000) and are highly endangered by deforestation (Myers et al. 2000; Klink and Machado 2005). Agriculture and livestock expansion are the main threat to

Communicated by Buckeridge.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00468-019-01815-8) contains supplementary material, which is available to authorized users.

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biodiversity in these ecosystems and effective conservation efforts are needed to avoid species extinction.

Besides those threats, global warming is a menace for all species in the tropical area. According to Sherwood and Fu (2014), by the year 2100, the global dryland area will be approximately 10% larger than today, mainly due to rainfall decrease in tropical and mid-latitude regions. Therefore, the ability to cope with this environment condition will be the key trait for species to thrive in a near future. Thus, desiccation tolerance is a key trait that will help species undergo extremely dry periods. Long-lived (desiccation tolerant) seeds maintain high viability for an extend period of time in determined storage conditions (Roberts 1973; Bonner 1990; Ellis 1991). Thus, seed banking is an efficient way to keep species safe, preventing plants from extinction. For this reason, the classification system regarding storage behaviour is a helpful tool to succeed in this endeavour.

Although the threshold among orthodox, recalcitrant, and intermediate behaviour in seeds is not always well defined (Daws et al. 2006; Walters 2015), several efforts have been taken to allocate species into these classes. The knowledge about seed storage behaviour is the first step for seed banking. In a restoration context, the information about desiccation tolerance is a crucial step for the success of the work, which ensures the maintenance of seed viability and high germination percentages when reintroduced to the wild.

Several studies have classified a great number of species from Atlantic Forest and Cerrado regarding seed desiccation tolerance/sensitivity and storage behaviour (Davide et al. 2003; Carvalho et al. 2006, 2008; José et al. 2007; Nery et al. 2014; Mayrinck et al. 2016). Thus, there is a need to assemble that information to understand seed storage capacity of the species living in these two biodiversity hotspots. This knowledge would create basis for establishing conservation efforts on endangered species, and, consequently, would help on reducing extinction risk.

In this study, we investigated 11 tree species (Table 1) due to their multiple uses in human activities and lack of studies on their seed storage behaviour. In addition, literature data were retrieved to gather information on seed desiccation tolerance/sensitivity for 79 species native to Atlantic Forest and Cerrado. Thus, the objectives of this study were (1) to classify the seed storage behaviour of 11 tree species and (2) to cluster information about desiccation tolerance/sensitivity for tree species native to two world's biodiversity hotspots Cerrado and Atlantic Forest.

Materials and methods

Fruit collection and processing

Fruits were collected between September of 2013 and November of 2015 in forest fragments of Alto Rio Grande watershed, nearby Lavras municipality, Minas Gerais, Brazil (21°14′30″S; 45°00′10″W) at 919 m a.s.l. (BRASIL 1992). The region is characterized as a transition area between the Atlantic Forest and Cerrado vegetation, with a prominent semideciduous seasonal rainforests (Van Den Berg and Oliveira-Filho 2000). According to Köppen's climatic classification, local climate is Cwa with characteristics of Cwb, presenting two seasons: dry, from April to September, and rainy, from October to March (Köppen 1936). Traits as colour, texture, and dehiscence were observed to collect mature fruits only. Fruits were hand processed immediately after collection (Davide et al. 1995) and the tests were performed immediately after processing (maximum 1 week later).

Table 1 List of species selected for this study and ecological information

Species	Family	Habit	Biome	Conservation status
Cedrela fissilis	Meliaceae	Tree	Cerrado/Atlantic Forest	Endangered
Ceiba speciosa	Malvaceae	Tree	Cerrado/Atlantic Forest	–
Cibistax antisyphilitica	Bignoniaceae	Tree	Cerrado/Atlantic Forest	–
Dalbergia miscolobium	Leguminosae–Papilionoideae	Tree	Cerrado	–
Eugenia pyriformis	Myrtaceae	Shrub/Tree	Cerrado/Atlantic Forest	–
Hymenaea courbaril	Leguminosae–Caesalpinioideae	Tree	Cerrado/Atlantic Forest	Least concern
Matayba elaeagnoides	Sapindaceae	Shrub/Tree	Cerrado/Atlantic Forest	–
Platypodium elegans	Leguminosae–Papilionoideae	Tree	Cerrado/Atlantic Forest	Least concern
Piptadenia gonoacantha	Leguminosae–Mimosoideae	Tree	Cerrado/Atlantic Forest	–
Qualea grandiflora	Vochysiaceae	Shrub/Tree	Cerrado/Atlantic Forest	–
Vismia brasiliensis	Hypericaceae	Shrub/Tree	Cerrado/Atlantic Forest	Endemic but without information

The conservation status data were collected from IUCN 2017/III Red List

Determination of seed water content

Seed water content (wc) was determined using four replicates of 0.5–6 g, depending on the average seed size for each species, in oven method at 103 °C for 17 h. Large seeds were cut into small pieces before weighing, to promote water loss. The results were expressed in fresh weigh basis (ISTA 2004).

Germination tests

Germination tests were conducted using four replicates of 25 seeds each, at 25 °C and constant light (cool white fluorescent tubes, 40 µmol m^{-2} s^{-1}). Large seeds (> 1 cm in the main axis) were placed in plastic trays (40 × 25 × 8.5 cm) with autoclaved sand moistened with distilled water. Small seeds (up to 1 cm in the main axis) were placed in Petri dishes on moistened germination paper. The trays were kept wet and the germination tests were conducted until all seeds were germinated or dead (rotted) (± 60 days). Seeds described as physically dormant in the literature were manually scarified using sandpaper before germination tests.

Seed classification

To classify seeds into the three classes (orthodox, intermediate, and recalcitrant), the methodology adapted from Hong and Ellis (1996) was utilized (Fig. 1). Freshly harvested seeds were subjected to germination test and assessed the seed wc. Then, seeds were dried to 12% wc and the germination was evaluated. If they remained viable, seeds were then dried to 8–5% wc, and germination was evaluated again. Viable seeds following drying to 8–5% wc were stored at − 18 °C for 90 days and were the germination assessed again.

Seeds were fast dried using activated silica gel (5 kg of silica gel) at a 20 °C, in a 'higrostat' box with forced ventilation, for large seeds, or into Gerbox® plastic container (90 g of silica gel) for small-sized seeds. The relative humidity was around 5% in both conditions, and silica gel was replaced when needed. For three species (*Platipodium*

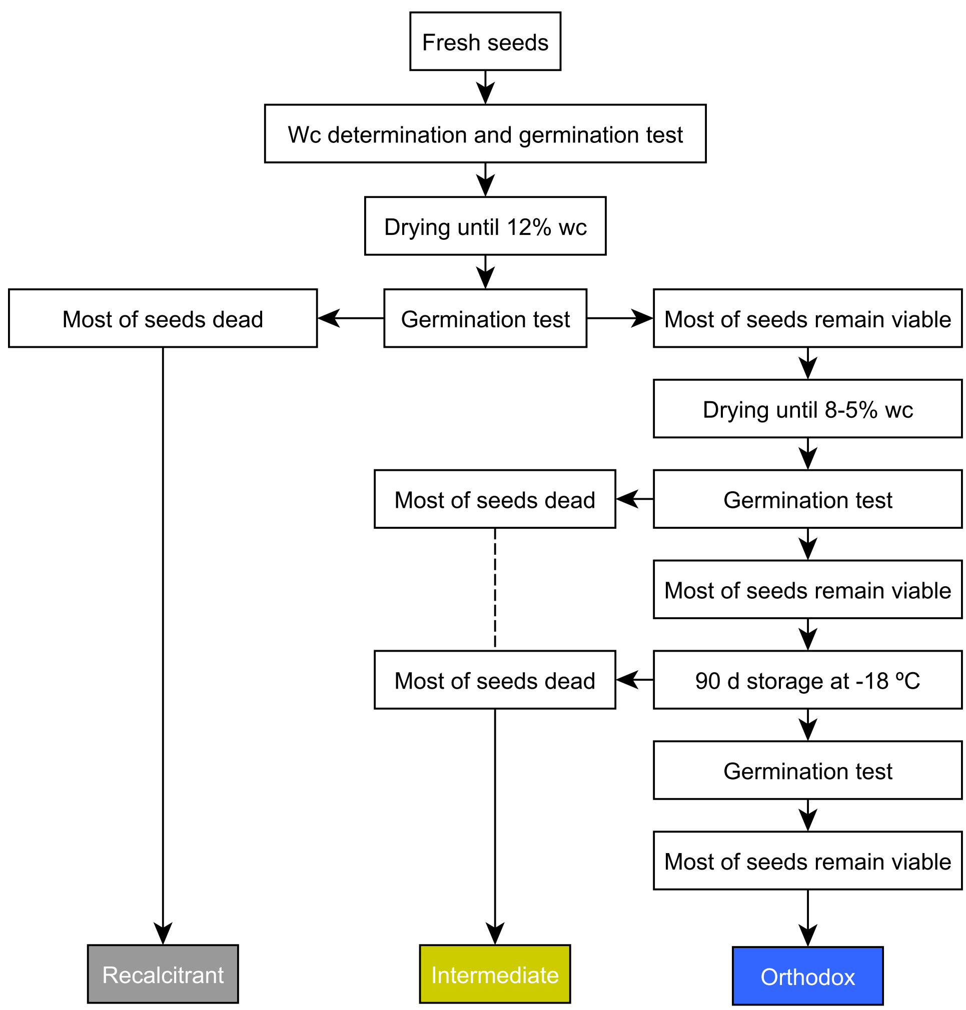

Fig. 1 Methodology for determination of seed storage behaviour adapted from Hong and Ellis (1996). *Wc* water content

elegans, Piptadenia gonoacantha, and *Qualea grandiflora*), seeds were also slow dried. Seeds were placed in single layer at plastic trays and stored at an acclimatised room at 20 °C and 60% of relative humidity. Seed wc was monitored daily until the two target weights, 12% and 8–5% wc, using Cromarty et al. (1982) equation. When the wc reached 8–5%, seeds were stored in plastic bags and placed at − 18 °C for 90 days, and then, the germination test was performed again.

Desiccation tolerance/sensitivity survey

Literature data were retrieved from studies on tree species from the Atlantic Forest and Cerrado biomes. Studies containing information about seed wc at the time of dispersal and seed storage behaviour were used in our work and the data clustered to investigate desiccation tolerance/sensitivity of seeds. Details on this data are further explained on supplementary material (Table S1). The purpose of this investigation was to explore desiccation tolerance/sensitivity trait on species native to these two tropical biodiversity hotspots.

Statistical analysis

All the data were submitted to normality (Shapiro–Wilk) and homoscedasticity (Bartlett) tests, followed by GLM (general linear models) analysis and Fisher's test at 5% probability using the R software for Windows (R Development Core Team 2014). All graphs were designed using the SigmaPlot® software (Systat Software Inc., San Jose, CA, USA).

Results

Seed classification

Seed storage behaviour is shown in Fig. 2. Seeds of *Cedrela fissilis, Cibistax anasyphilitica, Dalbergia miscolobium, Hymenaea courbaril, Platypodium elegans, Piptadenia gonoacantha*, and *Vismia brasliensis* were classified as orthodox. *Ceiba speciosa* seeds were probably orthodox. The seeds of this species were not stored at − 18 °C due to limited seed supply. Thus, we cannot confirm that *C. speciosa* seeds are orthodox. *Qualea grandiflora* seeds were possible intermediate, but further studies are need to confirm, since germination was very low in this study due to high incidence of embryoless seeds. Seeds of *Eugenia pyriformis* and *Matayba elaeagnoides* were classified as recalcitrant. *P. gonoacantha, P. elegans*, and *Q. grandiflora* were fast and slow dried and showed no significant germination responses between these two methods.

Desiccation tolerance/sensitivity survey

Data collected encompass the classification of seeds belonging to 30 different plant families (Fig. 3a). Leguminosae had the largest number of seeds classified (19 species), followed by Lauraceae, (10 species). For some families, information was found only for one species (e.g., Burseraceae, Calophyllaceae, Erythroxylaceae, and Hypericaceae). In Leguminosae ($n = 19$), 68.4% of species produced orthodox seeds, 21% intermediate seeds, and 10.5% recalcitrant seeds. In Lauraceae ($n = 10$), all species investigated produced recalcitrant seeds. For Myrtaceae ($n = 7$), 85.7% of species investigated produced recalcitrant seeds; 14.7% had intermediate seeds. In relation with the total percentage of species described ($n = 79$), 46.8% produced orthodox seeds, 19% intermediate, and 34.2% recalcitrant seeds (Fig. 3b).

Seed wc at the time of dispersal ranged greatly among the seed classes (Fig. 4). Mean wc found were 20.1 ± 10, 30.4 ± 13.7, and 49.8 ± 8.8 for orthodox, intermediate, and recalcitrant seeds, respectively. The minor variation in wc occurred for recalcitrant seeds; the lowest wc found in this seed class was 26.1%. These results are in agreement with other studies, showing that recalcitrant seeds are dispersed with higher wc than the intermediate and orthodox seeds (Hong and Ellis 1998; Mayrinck et al. 2016).

Discussion

Ecological trends of sensitivity/tolerance

There are several traits that distinguish desiccation tolerant seeds from those sensitive, such as high seed/coat ratio (SCR), induction of late embryogenic accumulating/abundant proteins, and the efficiency of antioxidant systems into the cells (Berjak and Pammenter 2013; Farnsworth 2000; Daws et al. 2006; Pelissari et al. 2018). Desiccation tolerance is a complex trait, under control of a variety of genes and individuals that have this trait have a common ancestor (Von Teichman and van Wyk 1994; Farnsworth 2000; Dickie and Pritchard 2002; Berjak and Pammenter 2008).

Furthermore, desiccation tolerance or sensitivity can be spatially distributed, as in tropical evergreen rain forest, 47% of species produce recalcitrant seeds (Tweddle et al. 2003; Daws et al. 2006). In fact, the trend of tropical areas having more recalcitrant species than other ecosystems types was demonstrated by several authors (Tweddle et al. 2003; Pritchard et al. 2004a; Lima et al. 2014; Pelissari et al. 2018). There is also a trend related to seasonality: recalcitrant species tend to shed its seeds on the wet season (Lima et al. 2014; Tweddle et al. 2003; Farnsworth 2000; Pritchard et al. 2004).

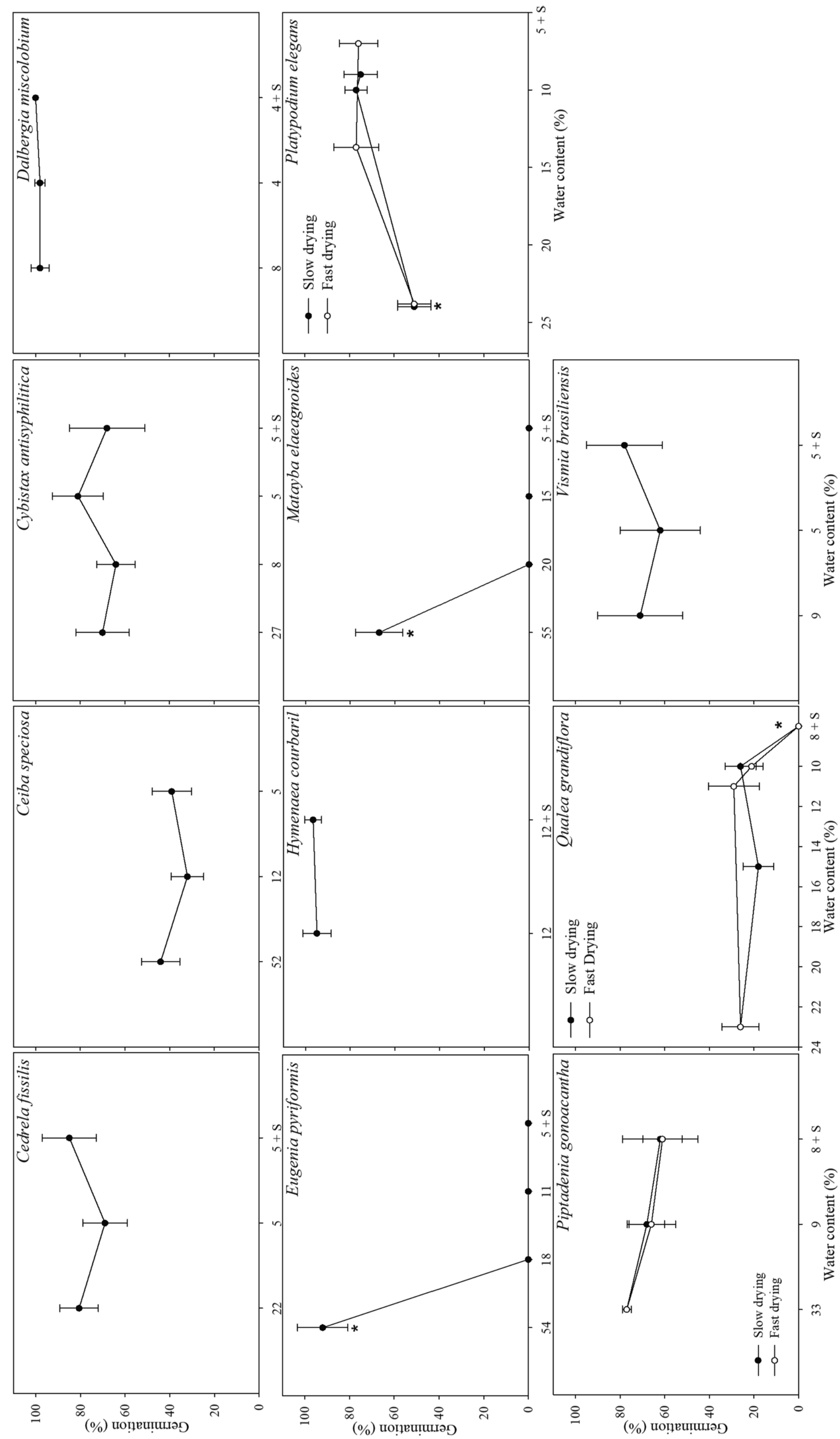

Fig. 2 Desiccation tolerance response of 11 tree species from Brazilian biodiversity hotspots (mean ± SD). Asterisks indicate significant difference among means, according to Fisher's test at 5% probability

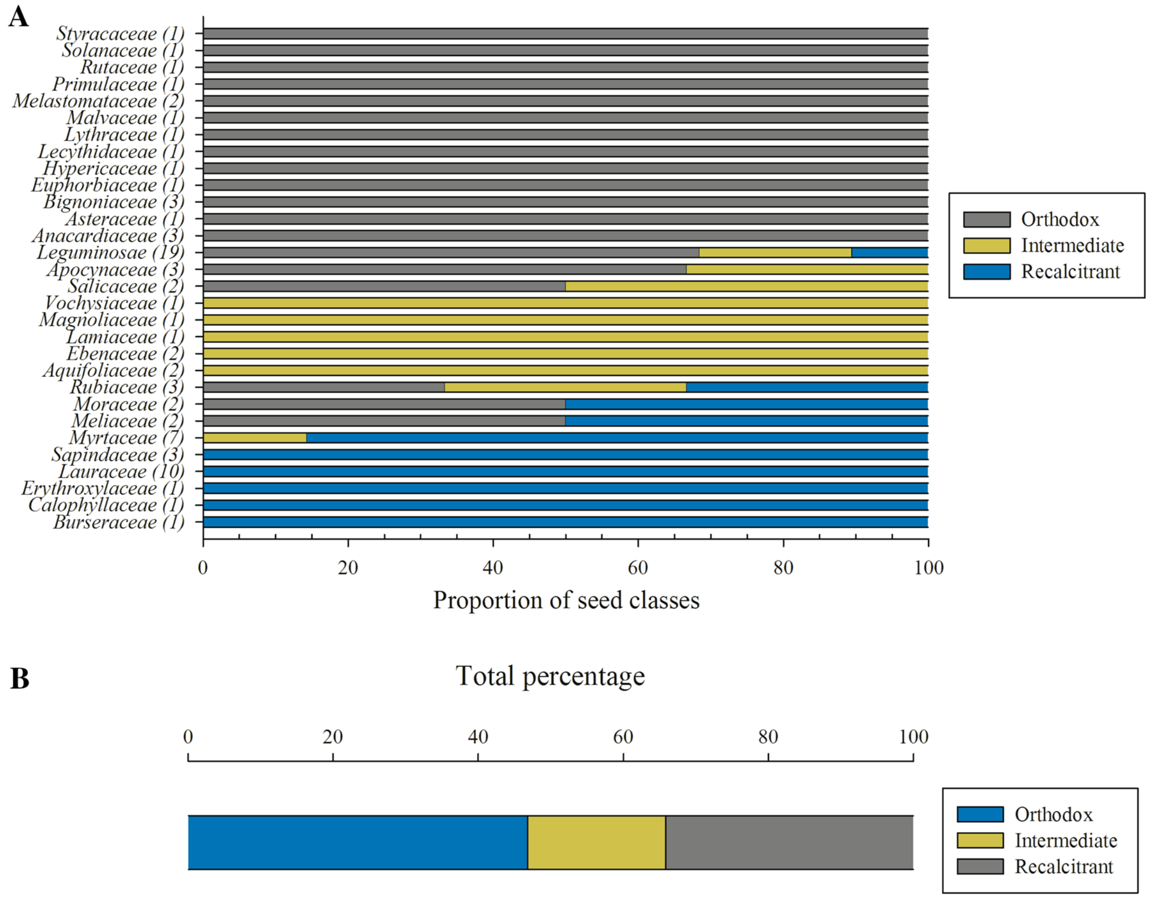

Fig. 3 **a** Seeds classification regarding desiccation tolerance/sensitivity grouped by plant families. Numbers in the top of the bars represent the number of species investigated. **b** Total percentage of seeds regarding desiccation tolerance/sensitivity. *N* = 79 species

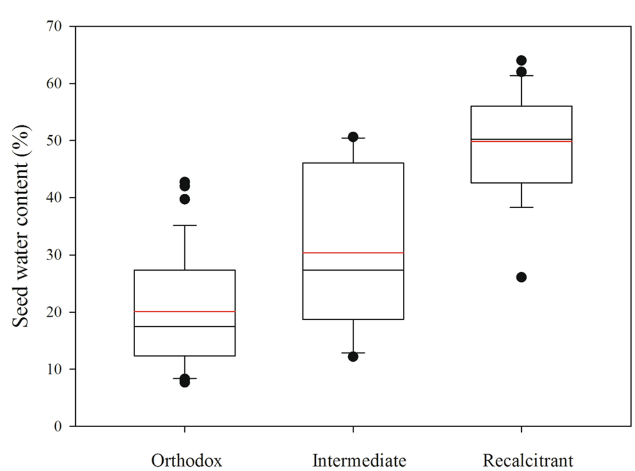

Fig. 4 Seed water content at the time of dispersal in each seed class regarding storage behaviour. Boxes represent the interquartile range (IQR) between first and third quartiles and the black line inside represents the median and the red line represents the mean. Circles indicate the outliers

As Tweddle et al. (2003) described, the number of species producing desiccation sensitive seeds reduce as drier is the climate. Thus, Cerrado tends to have more orthodox seeds and Atlantic Forest a higher percentage of recalcitrant seeds. However, the species producing recalcitrant seeds are still important for ecosystem balance in Cerrado as well. In Lauraceae family, all investigated species produced recalcitrant seeds. If this is a trend in this plant family, another conservation strategy should be taken into consideration rather than sub-zero storage, once recalcitrant seeds are damaged this way. In addition, Myrtaceae, one of the richest plant families in Atlantic Forest, had a high percentage of species producing recalcitrant seeds. This feature shows a possible obstacle to be faced in the conservation of tropical species.

Seeds conservation strategies

Alternatives to preserve non-orthodox species are conservation in botanic gardens (Pritchard et al. 2014), tissue culture, green houses, field planting (Walters et al. 2013), and the clonal orchards (Ruane and Sonnino 2006), but they require large areas and high maintenance costs, since care is needed to keep the individuals alive (irrigation, pests, and weed control). In vitro collections are problematic as well, since there is a risk of contamination and somaclonal variation, for example. The tissue culture technology represents two alternatives to preserve the germoplasm of recalcitrant species: the slow growth storage (Ruane and Sonnino 2006), for medium-term conservation (storage of plants at a few degrees above zero), and the cryogenic methods (Ruane and Sonnino 2006; Walters et al. 2013; Pritchard et al. 2014) for long-term storage.

The cryogenic storage is promising, despite presents a high implementation cost low maintenance is required (Ruane and Sonnino 2006; Walters et al. 2013). It comprises seed preservation in liquid nitrogen at extremely low temperatures (− 196 °C) after carefully dehydrate the seed tissue (Ruane and Sonnino 2006; Walters et al. 2013; Pritchard et al. 2014); thus, cryo-damage is avoided. It is more effective for orthodox seeds due to its smaller size in comparison with the recalcitrant seeds. Recalcitrant seeds are bigger, and its embryonic axis has to be extracted, dehydrated, and then treated with cryoprotectants, which is a challenge in several cases (Walters et al. 2013).

The best way to preserve species, especially non-orthodox seeds, would be in in situ conditions if species were not treated by deforestation. Some works have investigated in situ longevity of tropical recalcitrant seeds (Vaz et al. 2016, 2018; Marques et al. 2017) and the authors reported that seeds of two species remained viable after several months when maintained under in situ conditions. Thus, it could be a low cost and useful strategy to keep desiccation sensitive seeds alive for a longer period. For this, more studies must be carried out to extend the lifespan of the non-orthodox seeds longer than some months under in situ conditions.

Establishing living collections can also help to preserve species with recalcitrant seeds; however, for tree species, the need for large areas could limit the extent of this ex situ conservation strategy (Oldfield 2009). For those seeds that can be effectively stored, seed banking is an important way to keep seeds viable for long term and assure future uses (Thompson 1974; Linington 2003). Public institutions, like research institutes and botanical gardens, have a key role in these conservation efforts (Oldfield 2009; Pritchard et al. 2014; Teixido et al. 2017). The facilities in the underdeveloped countries are normally scarce, and if high proportion of native species have recalcitrant seeds, seed banking is hard task. In a recent work, Pritchard et al. (2014) detailed some recommendations for the conservation of trees, and one of them is to better understand the mechanism that controls desiccation tolerance in plants. Vaz et al. (2018) reported that some morphoanatomical traits in recalcitrant seeds, as a thickening in the embryo periclinal cell wall, may reduce water loss and consequently loss of viability. Associated with the beneficial effects of fruit tissues on seed germination and viability (Vaz et al. 2018), banking the whole fruit could be a useful tool to extent the longevity of recalcitrant seeds at a low cost. However, cryopreservation is the only applicable method for long-term conservation of recalcitrant seeds as far as we know (Berjak and Pammenter 2013; Walters et al. 2013). In addition, the information about seed biology of tree species is scarce, normally limited to economically important trees (Pritchard et al. 2014). Thus, the knowledge about seed storage behaviour, the first step for ex situ conservation, is essential to preserve ecologically important species and reduce the risk of extinction.

Most of the hotspots are located in the tropics (Myers et al. 2000), containing a large part of the global biodiversity. Besides the issues related to the high number of recalcitrant seeds (Pritchard et al. 2014), the conservation of these areas is limited. Among all hotspots identified by Myers et al. (2000), Cerrado is the one with the smallest protected area in the world: only 2.2% of its area is under legal protection, with more than 7000 endemic species (Klink and Machado 2005). In addition, Atlantic Forest has only 7% of its original area, with 8000 endemic species (Tabarelli et al. 2005). This information demonstrates the need for conservation efforts and further studies at those biomes.

In addition to deforestation, climate change is another threat to biodiversity and may trigger species loss. This is an issue that tree species from Cerrado and Atlantic Forest may face, shrinking plant distribution in these biomes (Siqueira and Peterson 2003; Colombo and Joly 2010). Two of the 11 species studied here are in the category 'Endangered' according to IUCN Red List [*Aspidosperma polyneuron* (Apocynaceae) and *Cedrela fissilis* (Meliaceae)]. Other species were classified as 'Lower risk/Least concern': *Copaifera langsdorffii* (Fabaceae), *Hymenaea courbaril* (Fabaceae), *Lafoensia pacari* (Lythraceae), *Magnolia ovata* (Magnoliaceae), *Persea pyrifolia* (Lauraceae), and *Senna macranthera* (Fabaceae).

Poor ecological information about seed storage for Brazilian species are still reported (Ribeiro et al. 2016), and huge efforts are needed to reduce this information gap, mainly for threatened species. In this regard, knowledge about seed storage behaviour of Brazilian threatened species is quite limited and crucial, and the immediate consequence is the extremely low number of species properly preserved in seed banks (Teixido et al. 2017). In the present study, we found that the two species with the status 'Endangered' produce orthodox seeds. In this case, these seeds can be easily stored, which facilitate ex situ conservation. However, conservation of species via seed banks is a long-term strategy (Ribeiro et al. 2016), and then, other actions are extremely important to avoid species loss.

Brazil is the richest country worldwide in number of tree species with the most significant number of endemic species (Beech et al. 2017). There are a lot of conservation efforts all over the world to keep biodiversity safe and seed banking is an essential tool. In our work, we evidenced a high percentage of recalcitrant seeds in two world's biodiversity hotspots, Atlantic Forest, and Cerrado. The initial seed wc right after dispersal can aid in the first care during the management of these species, and may indicate the subsequent steps to preserve the seeds. In a highly biodiverse country such as Brazil, significant efforts must be carried out to avoid tree species extinction. However, a small number of species are conserved in Brazilian seed banks yet.

Author contribution statement TAAV and ACD conceived and designed the experiments. LCV, TMP, and RCM performed the experiments. RCM, TAAV, and AGR-J wrote the paper.

Acknowledgements The authors would like to thank José Pedro for seed collection. LCV, RCM, and TMP thank PIBIC-FAPEMIG (Programa Institucional de Bolsas de Iniciação Científica da Fundação de Amparo à Pesquisa de Minas Gerais) for their scholarship. TAAV thanks CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and FAPEMIG (Fundação de Amparo à Pesquisa de Minas Gerais) for the scholarship. ACD thanks the CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for the research productivity granted.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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